Zea nicaraguensis (Poaceae), a New Teosinte from Pacific Coastal Nicaragua

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ABSTRACT. The geographically isolated annual teosinte from the coastal plain and embayments/estuaries near the Gulf of Fonseca, Nicaragua, is differentiated from Zea luxurians from southeastern Guatemala by its much longer and more abundant tassel branches, larger number of spikelets per branch, and longer, more pronouncedly transversely rugose outer glumes, as well as by its low-elevation coastal habitat. Molecular (ribosomal ITS) evidence and other data, placing it basal to Z. luxurians, seem to support this taxonomic segregation.

RESUMEN. El teosinte annual que crece en aislamiento geográfico en la planicie costera y los bajos inundados y esteros cerca del Golfo de Fonseca, Nicaragua, difiere de Z. luxurians del sureste de Guatemala por el número mayor de ramas y espiguillas por rama de la inflorescencia masculina, por la rugosidad transversal pronunciada de las glumas inferiores, además de altura baja de su hábitat costero. Evidencia molecular ubica a esta especie como más primitiva a la especie Z. luxurians y apoya a esta segregación taxonómica.

"There are very recent but as yet unverified reports of teosinte [in Honduras] from the mountains of the Department of Francisco Morázan, not far from Tegucigalpa, from the mountains of Copán, and even Nicaragua" (Standley, 1950: 61).

In November 1989, entomologist Allan H. Hruska, following up on a tip from Adrian Ramos, a fellow worker in the CARE Nicaragua maize improvement project, located a population of teosinte (a wild species of Zea) at Km 178 on the Chinandega–Somotillo highway in southwestern Nicaragua. Subsequently, ripe seeds were collected and, in 1990, sent to his mentor, Lowell ("Skip") R. Nault, eminent leafhopper taxonomist and maize virologist at the Ohio Agricultural Research and Development Center, Wooster, Ohio, who promptly

sent two of these to Iltis at the University of Wisconsin-Madison. Iltis, in turn, after noting their resemblance to those of Guatemalan Z. luxurians (Durieu & Ascherson) Bird, forwarded the two seeds to John Doebley (then at the University of Minnesota) for preliminary analysis. This revealed great morphological similarity to, but also considerable differences in developmental behavior from, Guatemalan teosinte.

The general area of Hruska's 1989 discovery in southwest Nicaragua was visited by the authors on 5 October 1991. No teosinte was encountered there; however, repeated inquiry about the location of additional stands of "teosinto," the local name, hinted at by Hruska in a letter, led us several days later to the discovery of a small population some two hours by horse from Rancho Apacunca, some 19 km to the west of Hruska's site. Now evidently extremely local and rare, the teosinte at this location is remarkable for its ability to grow in as much as 0.4 m of standing or slowly moving water.

Zea nicaraguensis Iltis & Benz, sp. nov. TYPE: Nicaragua. Chinandega: Pacific coastal plain near Golfo de Fonseca, edge of now flooded [by mid-December, bone-dry] area between Estero Paimica and Estero Palo Blanco, at a place seasonally occupied by cattle herders known as El Rodeo (12°53′45″N, 86°59′W), ca. 4–5 km NNW of Apacunca (12°52′30″N, 86°57–58′ W), 18–20 km SW of Villa Nueva, alt. 9 m, 8 Oct. 1991, H. H. Iltis, B. F. Benz & A. Grijalva 30831 (holotype, HNMN; isotypes, K, MEXU, MO, NY, US, WIS-2).

Topotypic paratype of same population, in ripe fruit, 18 Dec 1991, H. H. Iltis, M. Castrillo, C. Medina & C. Aker 30919 (HNMN, WIS).

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Similis Zeae luxurianti, sed robustior, culmis ad bases 3–5 cm diam., 2–4(–5) m altis, inflorescentiis masculinis robustioribus et 23–32 cm longis, cum 27–38 ramis, differt.

Maize-like erect annuals, unbranched to candelabra-branched, 2-4(-5) m tall (Fig. 1A), sometimes with 1 to 4 stout basal tillers (suckers), these to 2 m long in giant plants, with prominent prop roots (Fig. 1D). Male inflorescences (tassels) 23-32 cm long, with 27-38 slender branches (including infrequent secondary branches from the base of basal primary ones), the central one undifferentiated [all plants of the type not quite mature as of date of collection (8 Oct.), hence weak, with all the branches drooping downward together on one side] (Fig. 1B); branches each with ca. 36 to 64 sessilepedicellate spikelet pairs, the outer glumes with two prominent keels that merge at the apex, ca. 9-11 mm long, strongly transverse rugulose especially when young (Fig. 1C); culms (tassel peduncles) immature in the type specimens, only ca. 3-6 cm long, but dramatically elongating to 25 cm or more by maturity; tassel branching axes variable, 8-12 cm long. Female spikes in sheathed complex clusters, 6–18 cm long, on peduncles of variable length, enclosed by glabrous, linear-lanceolate spathes, these 6-10 cm long; fruitcases ca. 4 to 10 per spike, trapezoidal appressed-cylindric, very smooth and shiny, ± uniformly colored a light to dark (coffee or earthen) brown, 7–10 mm on the long (glume) side, 3-6 mm on the short side, 4-6 mm diam. (Fig. 1C).

Flowering (tasseling) from mid-October to early November, with fruitcases mature in mid-December. Common name "Teosinto."

The still somewhat immature tassel of one of the two WIS isotypes (Fig. 1B), symbolized by the second highest filled circle on Figure 2, was used in 1992 for the University of Wisconsin Herbarium's traditional New Year's card, photocopied directly and unreduced from the specimen onto herbariumsize sheets and sent to over 400 herbaria, botanists, and friends all over the world.

Distribution, ecology, and habitat. (All locations on lower half of Nicaragua topographic sheet Villa Nueva 1:50,000, 1989): Zea nicaraguensis appears to be restricted to the Department of Chinandega, Nicaragua, in the lowlands of the Gulf of Fonseca that drain to the nearby Pacific Ocean, at elevations of 9 m (type collection) to 75 m (according to Hruska's seed collection, presumably from near Israel; see below). We were told by some local old campesinos that this very flat landscape was once covered mostly by savannas of Crescentia, with gallery

forests only near the confluence and levees of seasonal streams.

(1) The Apacunca (holotype) locality: The nearby savannas had in the past often been cleared for agriculture, once for rice, then for pasture, and are now heavily grazed by cattle. At the October date of collection, this vast treeless plain was under 0.2-1.5 m of very slow-moving water but deceptively covered with a dense, lush, and green, rooted floating mat of mostly introduced Old World and some native New World grasses, such as Brachiaria mutica (Forsskål) Stapf, Echinochloa polystachya (HBK) Hitchcock, E. pyramidalis (Lamarck) Hitchcock & Chase, Oryza latifolia Desvaux, Paspalum virgatum L., and Hymenachne amplexicaulis (Rudge) Nees, as well as colonies of Neptunia sp., Thalia geniculata L., and Echinodorus paniculatus Micheli, the last two often locally dominant. The dense gallery forest, where the teosinte grew, was located on a slightly higher river levee, which formed somewhat of an island, where, inaccessible to cattle during flooding, the teosinte was thus protected especially in its early stages from grazing (Fig. 3). Teosinte, now rare, was reported by the old cowboys at Rancho Apacunca to have been "ubiquitous" here in the past.

With floodplain savanna on one side, and a seasonal flooding river (estero) on the other, the strip of gallery forest of Ceiba pentandra (L.) Gaertner, Pithecellobium dulce (Roxburgh) Bentham, Enterolobium cyclocarpum (Jacquin) Bentham, and Bravaisia integerrima (Sprengel) Standley had an understory of Coccoloba (2 spp.), Bactris minor Jacquin, Cassia reticulata L., Caesalpinia spp., and Crescentia alata HBK, and here, also, towering thickets of gigantic plants of teosinte. Growing both in shade and on the forest's sunny margins, their stems and prop roots were covered by shallow standing water 10-40 cm deep, this by 8 October beginning to recede (Fig. 1D). But only a very few of the several hundred teosinte plants were now starting to "shoot out" their male inflorescences, and, despite diligent searching, all we could find were nine somewhat immature tassels, which became the type collection (see Discussion).

(2) The Cayanlipe locality (for paratype and second population) lies in the flat, mostly treeless Comarca Cayanlipe 4 km south and east of the village of Cayanlipe in the Llano de Toreras and 7 km east-southeast of the Apacunca station. Although this area gets flooded as well as during the rainy season, the dirt road nearby is not elevated like the one leading to Rancho Apacunca, a circumstance that prevented us from visiting this teosinte population in October. Zea plants here are ca. 3.0–3.5

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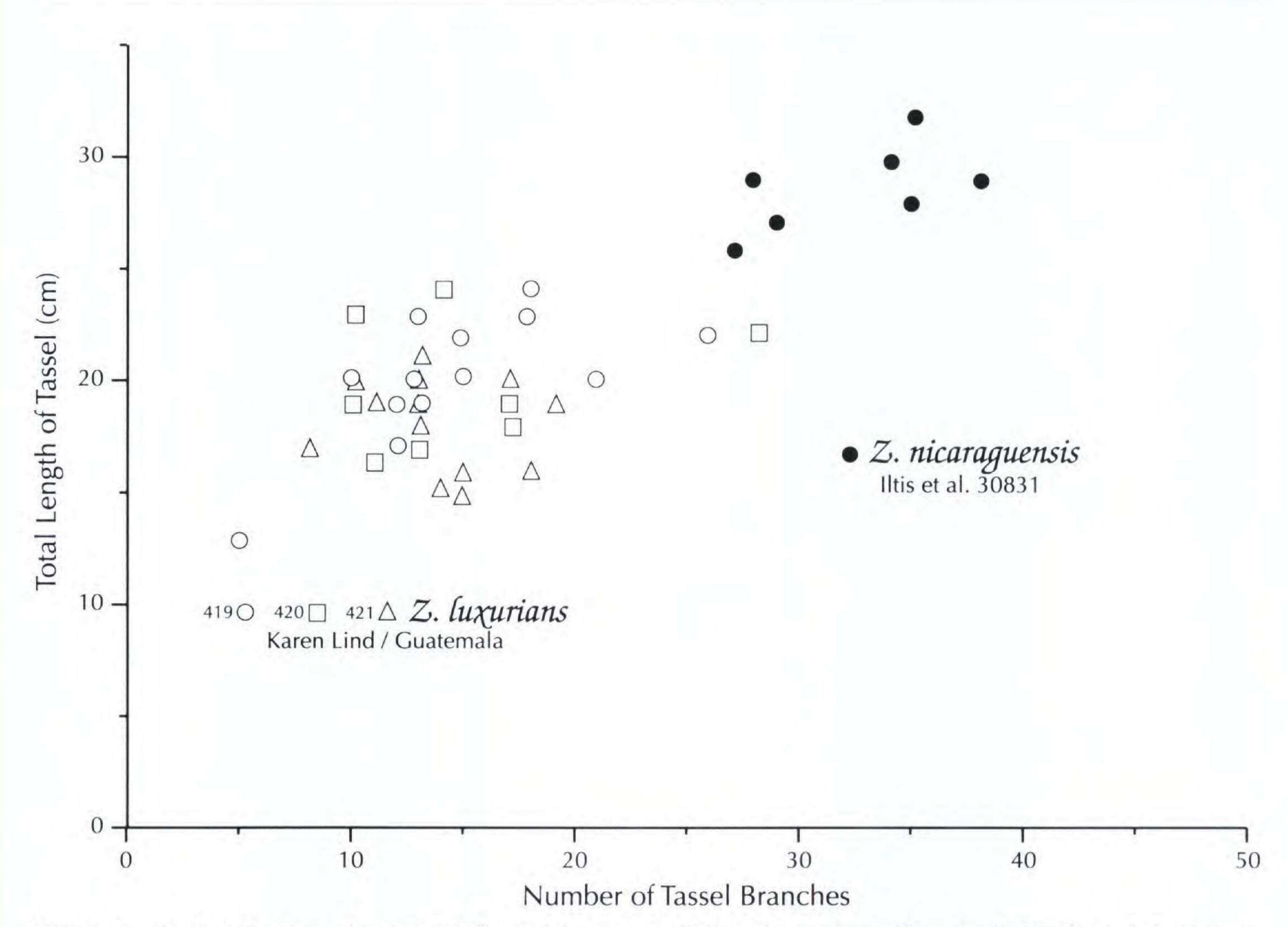


Figure 2. Scatter diagram of seven (of the eight) isotypes of *Z. nicaraguensis* (*Iltis et al. 30831*) and three mass collections of *Z. luxurians* [based on *K. Lind 419, 420*, and 421 from the vicinity of El Progreso, Dept. Jutiapa, Guatemala (location data in Doebley, 1983: 36; specimens in WIS)].

m tall, unbranched or some with long upper candelabra branches. A few had up to 4 basal shoots (tillers), and all were now past fruiting on 18 December, the date of collection, with their tassel branches mostly disarticulated. The now bone-dry savanna of jicaro, *Crescentia alata* HBK, and scattered *Guazuma ulmifolia* Lamarck was covered by solid stands of the African *Hyparrhenia rufa* (Nees) Stapf. At this location, the *Zea* population was marginalized to a dense, weedy, spiny thicket of *Byttneria aculeata* (Jacquin) Jacquin and *Acacia farnesiana* (L.) Willdenow, where, safe from cattle, it survives in a small colony of less than 20 individuals.

(3) Israel, Nicaragua: In 1991, A. H. Hruska wrote to L. R. Nault that he had located teosinte on 7 Nov. 1989 "... in tassel"... at km 178 [from

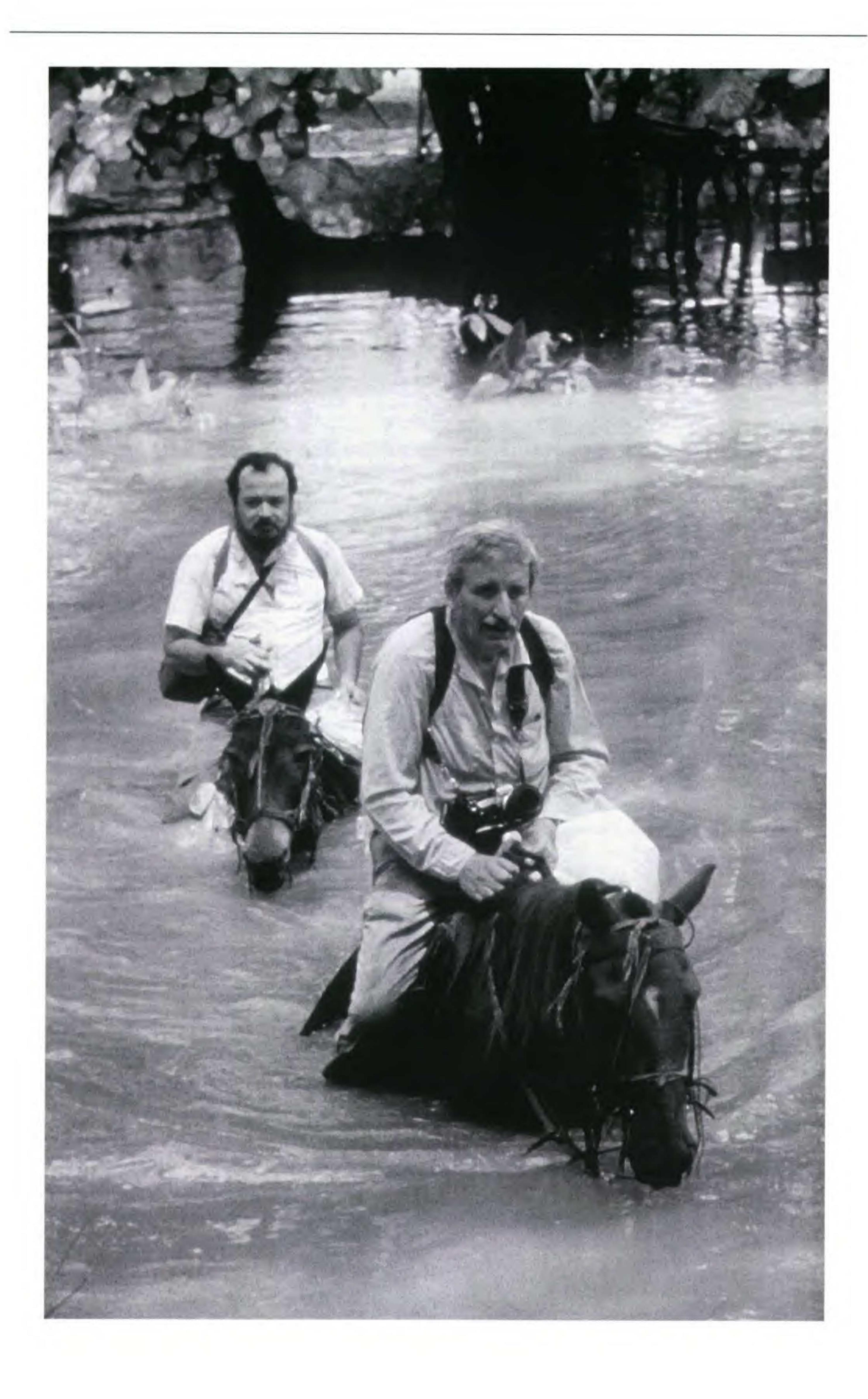
Managua] of the Chinandega–Somotillo highway at elevation of about 75 m, in dry jicaro (calabash) savanna forest on very heavy clay. . . . From all indication this is not a recently introduced population, for peasants around there say it's a well known plant, that has always been here. . . . There was lots more where this came from." (From copy of letter, in WIS!)

There is some question concerning the exact location of Hruska's population. Location Km 178 lies at an elevation of ca. 20 m, as is the land surrounding the village of Israel, which was not visited by us, hidden behind some hills 2 km from the highway to the southeast. We suspect that Hruska's teosinte came from the savanna-covered flatlands only 11–15 m in elevation, located 1–6 km south and east on the dirt road to Mina El Limon, espe-

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Figure 1. Zea nicaraguensis Iltis & Benz at the type locality (18 Dec. 1991). —A. Dense thicket of dry, overmature, mostly unbranched, 3–5 m tall plants, with tassels (0.2–0.4 m long) mostly disarticulated and missing. Cony Navaez, curator of UNAN-Leon Herbarium, standing. —B. Young tassel, with lax branches drooping over on one side, before elongation of the culm, i.e., the ultimate and often very long internode just beneath the tassel. (8 Oct. 1991). —C. Mature fruitcases and overmature tassel branches of A. —D. Prop roots of A. (A, C, D, Iltis et al. 30919; B, Iltis et al. 30831.)

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cially in areas marked on the map as Llano El Coyol, Sitios de Algodon, and Laguna El Tule. While northeast of Israel the topographic map shows many scattered 20–40(–161) m high and very steep cliffs jutting out of the plain (and there was even one adjacent to the highway near Km 178, which we climbed), these, it would seem, would be unlikely habitats for *Zea nicaraguensis*. In any case, intensive fieldwork in this "botanically promised land" of Israel, Nicaragua, would be highly desirable.

There exists a herbarium specimen, collected on 19 September 1990, grown from Hruska's seeds (Doebley 648, MIN), the label data of which state that: "Plants grown in a growth chamber at the University of Minnesota, produced mature seeds four months after planting, this much more rapidly than is typical of . . . [Zea luxurians]. This collection, clearly differentiated from the Guatemalan form of this species by its small stature and early maturity, may represent a new subspecies." In addition, of course, it may simply show how enormously sensitive in their responses to moisture, daylength, and altitude annual teosinte plants can be. (See below; also Bird, 2000; Iltis, 1983, 1987, 2000.)

Paratypes. NICARAGUA. Chinendaga: Pacific coastal plain (planice costera) near Golfo de Fonseca, just S of Comarca Cayanlipe (a vast Sorghum-cultivated, treeless plain) at a place locally called "La Tronconado," 3 km S of village of Cayanlipe, 14 km SW of Villa Nueva, 12°52′25″N, 86°54′50″W, alt. 15 m, 16 Dec. 1991 (fr), H. H. Iltis, M. Castrillo & C. Medina 30900 (WIS); re-collection of the holotype population (see above), 18 Dec. 1991 (fr), H. H. Iltis, M. Castrillo, C. Medina & C. Aker 30919 (HNMN, WIS), with a 2 kilo total of bulked seed germ plasm of same deposited in the germ plasm banks of the International Center for Maize and Wheat Improvement, Texcoco, Mexico, I.D. CIMMYT 13451, fide S. Taba (11083, fide Bird, 2000); the Nicaraguan Agricultural University (UNA), Managua; the U.S.D.A., Northcentral Regional Plant Introduction Station (NC7), Ames, Iowa, I.D. Ames 21893; and John Doebley, now in Madison at the University of Wisconsin's Genetics Department.

Ethnobotanical notes on "Teosinto." On 8 October 1991 at Rancho Apacunca, Felix Valenidaceda indicated that "teosinto" is consumed by cattle only when young. When mature, the plant is used to make ramadas [fences, shelters, or roofs perhaps]. Valenidaceda told us that "from 7 to 10 years ago, the area from El Jicote to El Rodeo to Los Pozitos was covered by teosinto, common enough to be

dominant in the local vegetation. Cattle grazing has always been practiced in this region. . . ", though in the more recent past it has become a year-round enterprise, probably correlated with the construction of the prominently elevated gravel road to Rancho Apacunca. Apparently "...10, maybe 15 years ago Apacunca was not occupied year round; it was inhabited only during the summer months because water then becomes available. . ." hence the name (on the 1961 topographic sheet made from 1954 aerial photos) Veraneadero Apacunca. (Note: the 1989 topographic map Villa Nueva 1:50,000 gives just plain Apancunca—the n evidently in error the omission of Veraneadero suggesting full-year occupancy.) "The people moved seasonally from a community, called La Mesa, near Somotillo, ca. 12 km to the north, to Apacunca in April or May, when it begins to rain. They stayed until December (or longer, depending on water availability) and then returned to La Mesa until May. In the lowlands, i.e., Apacunca, they tended a few cattle and raised corn." This information comes from local campesinos, all men, who indicated that when "teosinto" was encountered in their plots, presumably slash and burn, the cattle consumed it as fodder. Implicit in this description (which was specified by Achiles Peralta, a citizen of the village of Israel) was the observation that when the people finally settled in Apacunca year-round and maintained large herds of cattle and planted crops other than corn, i.e., rice, the teosinte became scarce (cf. Wilkes in litt. about a similar situation in the Valley of Mexico).

KEY TO THE ANNUAL SPECIES OF ZEA SECTION LUXURIAN-TES DOEBLEY & ILTIS

(Organized to fit into the key in Doebley & Iltis, 1980: 991, underneath the number 2 couplet).

- 2a. Tassels 12–24 cm long, the branches rather stiffly ascending; number of tassel branches (4–)10–28, each 7–21 cm long; central tassel branching space (or axis) short, (1–)3–6(–9) cm long; number of spikelet pairs per primary tassel branch 20–35 or fewer; length of culm (peduncle) (10–)12–20(–23) cm long; Mexico (Oaxaca), southeast Guatemala, Honduras (Choluteca) . . .
- 2a. Tassels (23-immature) 26-32 cm long, the branches relatively lax and drooping; number of tassel branches 27-38, each 13-28 cm long or longer; central tassel branching space (8-)10-12

Figure 3. Hunting teosinte in Nicaragua. Alfredo Grijalva, Herbarium curator at UCA, Managua, Nicaragua, and Hugh H. Iltis (in front), Director of WIS, accompanied by Bruce Benz, Assistant Professor of Biology at Texas Wesleyan University, Ft. Worth, Texas (who took the photograph), crossing a gallery forest on the broad, flat, seasonally flooded lowlands inland from the Golfo de Fonseca on the Pacific Ocean in Depto. Chinandega, in southwestern Nicaragua near the Honduran border. Photo Bruce Benz.

DISCUSSION

The closest relative of Zea nicaraguensis is clearly Z. luxurians of southeastern Guatemala (Doebley & Iltis, 1980; Doebley, 1983; Iltis et al., 1986), an annual with similar, strongly two-nerved lower glumes. But, as the above key and Figure 2 show, the primary tassels of Z. luxurians are smaller in many ways than those of Z. nicaraguensis, differing in tassel length (12-24 vs. 23-32 cm), number of tassel branches (4-28 vs. 27-38), central tassel branching space (1-9 vs. 8-12 cm), and number of spikelet pairs per branch (ca. 20-35 vs. 36-64). Moreover, the primary tassels of the type specimens are all still immature (Fig. 1B): (1) their spikelets are all closed, and not anywhere near anthesis; (2) the lower quarter of the tassels, their branches still tightly enveloped by the uppermost leaf sheath for 6-8 cm, are still only the palest green, with the exposed ends of the branches still lax and drooping off together and sideways (Fig. 1B); and (3) even more immature are the markedly undeveloped tassel culms, that is, the ultimate, generally very long internode beneath the male inflorescences: in the seven (out of the nine) type specimens measured, they are only 2.5-5.6 cm long, soft and pale yellow, and are yet to dramatically elongate to their full length sometime just before anthesis. Fortunately, we do have, from this same population, one fully mature peduncle, collected on 18 December 1991, the day we returned to collect 2 kilograms of ripe seed germ plasm from this, now weather- and animal-devastated, population (Fig. 1A). This single "corpse" of a tassel is borne on a culm fully 25.4 cm long (!), with the tassel itself, however, reduced to its axis and a few short branch stubs. Such a long culm (or even longer as suggested by Fig. 1A) is what one would expect, in comparison to the shorter culm length range (10-23 cm) of the Guatemalan Z. luxurians. Thus what a fully mature Nicaraguan teosinte tassel would look like in all its glory, we can only guess. But with tassels over 40 cm in diameter, it surely must be a beautiful sight.

While our limited measurements of Z. luxurians spikelets agree well with those provided by Doebley (1983), this by far the most sophisticated mathematical analysis of the Zea male inflorescence ever, our values for Z. nicaraguensis clearly exceed his numbers for Z. luxurians. Unfortunately, because of

our collection's immaturity, we did not measure many of the characters he employed, a task that must be left to others at a time when better fieldcollected material of this species will become available.

Molecular evidence. Recently, Buckler and Holtsford (1996) demonstrated from ribosomal ITS (internal transcribed spacer) evidence that within the Luxurians clade, the Nicaraguan teosintes from Chinandega (our Z. nicaraguensis from near Apacunca) are basal to the Chiquimula teosintes from Guatemala (Z. luxurians), a finding of considerable interest.

Environment versus genetics, the unknown in the equation. How much of the large size of the Z. nicaraguensis tassels, and of the Nicaraguan teosinte plants as a whole, is due to the moist habitat and how much to genetics, is at present unanswerable. Certainly, wild Zea species are enormously sensitive to even the slightest environmental changes in daylength and moisture, as Iltis (1983, 1987, 2000) has repeatedly described in regard to tillering and branching. Bird (2000) recently demonstrated this experimentally with Z. nicaraguensis, grown in Mexico City and North Carolina from topotypic seeds (Iltis et al. 30831), producing bizarre plants not resembling the native grown material whatsoever. The label data of Doebley 648, grown in Minneapolis and cited above, make the same point.

How would natural selection act on such easily modifiable and labile phenotypes? For teosinte, the environment brings out unsuspected, genetically based potentials, with the genotype essentially remaining the same (Iltis, 1983: 892). Continued, directional selection would increase this potential to the point where it will become genetically assimilated (Waddington, 1957) by what Mayr (1970: 110–111) calls threshold selection, which allows certain cryptic genes to become expressed. Speciation, by way of a founder population in geographic isolation, such as here in Nicaragua, might thus soon occur.

While we do not know the chromosome number of Z. nicaraguensis (probably diploid like Z. luxurians, with n = 10), nor the degree of interfertility between Z. nicaraguensis and Zea mays L. subsp. mays, with no such hybrids known, we anticipate that this species will provide maize breeders with a potentially valuable source of germ plasm that may lead to the development of maize capable of growing in water-logged soils.

Finally, it was the desire to see fully mature flowering material of the Nicaraguan populations that caused us to delay publishing, until events beyond our control have now forced the issue. Although collecting this population at the right time would have its problems (the area was land-mined during the recent Contra war), it would have its rewards as well. We may only hope that now, with the appearance of the *Flora de Nicaragua* (Stevens et al., 2000), the ever-larger contingent of well-trained Nicaraguan botanists and environmentalists, with aid from conservationists worldwide, will take up this challenge and work hard to have these wild populations of teosinte preserved, if at all possible, in situ (Guzman & Iltis, 1991). It should and can be done! Long live Nicaraguan biodiversity!

[Postscript: The Honduran Collection of P. C. Standley: This remarkably prolific collector of the Mesoamerican flora discovered a teosinte in 1949 at San Antonio de Padua, Department of Choluteca, Honduras, at 850 m (Standley, 1950) (P. C. Standley & J. de Dios Cruz 24677), a station not much more than 90 km north from those we located in Nicaragua. Standley's herbarium material (in F, UC, US), relegated to Z. luxurians by Wilkes (1967), Doebley and Iltis (1980), and Doebley (1983), includes old tassels that suggest affinity to the Guatemalan populations. On 17 October 1991, the first author traveled the length of the valley east of Pespire up to San Antonio de Padua, but had no success in locating any teosinte. However, at Pespire and localities to the east of it, a number of informants (six out of ten, all older men) instantly recognized fruitcases of teosinte shown to them as "ah, sí, es maíz café" or "maizena," local names of a plant which, they said, "used to grow abundantly here thirty years ago and was sometimes cultivated as a coffee substitute." Some even said it used to be planted (sembrar), but at San Antonio, where the road ends high up in the mountains, no one seemed to know it. Admittedly, it was nearly dark when we arrived and informants were scarce. The two other collections from San Antonio, cited by Doebley (1983: 37) as Z. luxurians [Freytag s.n. (MO) and Molina 5881, 5882 (US)], were not now available to us, but at the time of our collaboration (Doebley & Iltis, 1980) we must have thought them well within the range of variability of Z. luxurians.]

Acknowledgments. Thanks are due first of all to the perceptive Adrian Ramos and Allan Hruska of CARE Nicaragua, the discoverers of teosinte in Nicaragua; to Lowell Nault, who conveyed two fruitcases to us; and to John Doebley, who grew them out and made preliminary observations: to all, our appreciation. We must next gratefully acknowledge the help of our botanical colleagues at the National Herbarium of Nicaragua, Managua (HNMN), CrisAlfredo Grijalva, its Director, who without protest drove us twice in one week from Managua to Chinandega and thus ensured our success in locating the new teosinte. At Rancho Apacunco we were aided by Conrado Moradez and Sr. Tinoco, the owner of the land, who gave us permission to collect and graciously allowed us to borrow his horses and his well-armed guides. Reaching back in time, we are grateful to my former student and Guatemalan botanist, Karen Lind, for the three population samples of *Z. luxurians* collected, at the first author's request, near El Progreso, Jutiapa, Guatemala, in 1978.

For help during the Honduran excursion to relocate Standley's maiz café, the first author much enjoyed the hospitality of the Escuela Agrícola PanAmericana at Zamorano and the aid given there by George Pilz, and especially Roberto Young and Ramon Zuniga, both of the latter invaluable and stimulating field companions. Editorial comments on the manuscript by Ted Cochrane and an anonymous reviewer were much appreciated, as was the naming of our grass collections by Gerrit Davidse. Finally, this research was supported by the Nave Bequest to the Latin American Studies Program of the University of Wisconsin-Madison and by the O. N. and E. K. Allen Fund of the U.W. Herbarium (WIS). The illustrations were expertly prepared by Kandis Elliot and the manuscript by Loraine Stribley of the U.W. Botany Department and by Liz Levitt, undergraduate student in the U.W. Zoology Department: to our thanks we add our affection.

Literature Cited

Bird, R. M. 2000. A remarkable new teosinte from Nicaragua: Growth and treatment of progeny. Maize Cooperation Genetics Newsl. 74: 58–59.

Buckler, E. S., IV & T. P. Holtsford. 1996. Zea systematics: Ribosomal ITS evidence. Molec. Biol. Evol. 13: 612–622.

Doebley, J. F. 1983. The maize and teosinte male inflorescence: A numerical taxonomic study. Ann. Missouri Bot. Gard. 70: 32–70.

—— & H. H. Iltis. 1980. The taxonomy of Zea (Gramineae). I. Subgeneric classification with key to taxa. Amer. J. Bot. 67: 982–993.

Guzman, M. R. & H. H. Iltis. 1991. Biosphere Reserve established in Mexico to protect rare maize relative [Zea diploperennis]. Diversity 7(1 and 2): 82–84. [Spanish edition, Diversity 7(1 and 2): 89–92.]

Iltis, H. H. 1983. From teosinte to maize: The catastrophic sexual transmutation. Science 222: 886–894.

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- ———. 2000. Homeotic sexual translocations and the origin of maize (*Zea mays*, Poaceae): A new look at an old problem. Econ. Bot. 54: 7–42.
- ——, D. A. Kolterman & B. F. Benz. 1986. Accurate documentation of germ plasm: The lost Guatemalan teosintes (*Zea*, Gramineae). Econ. Bot. 40: 69–77.
- Mayr, E. 1970. Populations, Species and Evolution. Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts.
- Standley, P. C. 1950. Teosinte in Honduras. Ceiba 1: 58–61. Stevens, W. D., C. Ulloa Ulloa, A. Pool & O. M. Montiel (editors). 2000. Flora de Nicaragua. Monogr. Syst. Bot. Missouri Bot. Gard. 80.
- Waddington, C. H. 1957. The Strategy of the Genes. Allen & Unwin, London.
- Wilkes, H. G. 1967. Teosinte: The closest relative of maize. The Bussey Institution of Harvard University, Cambridge, Massachusetts.